

Effects of soil moisture and light intensity on ecophysiological characteristics of *Amorpha fruticosa* seedlings

ZHANG Xiu-ru • TAN Xiang-feng • WANG Ren-qing
XU Nan-nan • GUO Wei-hua

Received: 2012-02-06;

Accepted: 2012-08-25

© Northeast Forestry University and Springer-Verlag Berlin Heidelberg 2013

Abstract: We investigated the combined effects of soil moisture and light intensity on the growth, development and ecophysiological characteristics of one-year old *Amorpha fruticosa* seedlings. Soil moisture and light intensity influenced the ecophysiological characteristics of *Amorpha fruticosa* seedlings. Soil moisture resulted in the decreases of growth rate, individual size, net photosynthetic rate, transpiration rate, leaf water loss rate (WLR), and biomass accumulation of plant parts, and led to increased leaf water saturation deficit (WSD). Under water stress, more photosynthetic products were allocated to root growth. With decreasing light intensity, net photosynthetic rate, transpiration rate, chl_a/b, water saturation deficit, water use efficiency, water loss rate and biomass accumulation declined, while Chl_a, Chl_b, Chl_a+b and carotenoids (Car) increased and more photosynthetic products were allocated to stem and leaf growth. Maximum growth vigor, net photosynthetic rate and total biomass accumulation in *Amorpha fruticosa* seedlings was recorded at 75–80% soil water-holding capacity and 100% light density in greenhouse environments.

Keywords: *Amorpha fruticosa*; ecophysiological characteristics; light intensity; seedling; soil moisture

Fund project: This work was financially supported by National Science Foundation of China (No.31270374), Independent Innovation Foundation of Shandong University (No.2011DX008) and Natural Science Foundation of Shandong Province, China (No.2009ZRB01875; ZR2010CM062).

The online version is available at <http://www.springerlink.com>

ZHANG Xiu-ru • TAN Xiang-feng • WANG Ren-qing • XU Nan-nan • GUO Wei-hua (✉)

Institute of Ecology and Biodiversity, College of Life Sciences, Shandong University, Jinan, 250100, P. R. China.

Email: guo_wh@yahoo.com

ZHANG Xiu-ru

Clinical College of Tianjin Medical University, Tianjin, 300270, P. R. China.

Corresponding editor: Hu Yanbo

Introduction

Soil moisture and light intensity are important ecological factors that affect the growth and distribution of vegetation. Generally, the two factors influence the ecophysiological processes of plants, such as photosynthesis, transpiration and organic matter transport, thereby affecting water and light use efficiency of plants (Zhang et al. 2004; Pell et al. 2007). With the reduction of the atmospheric ozone layer, the role of light as an environmental stress factor becomes increasingly prominent (Bertamini and Neduncheanian 2003). Drought and water shortage are considered the most critical ecological limiting factors for vegetation restoration and production in agroforestry, and with the further intensified water crisis and drought hazards, water-saving strategies in agroforestry have received increasing attention. Plant adaptations to drought and light stress caused by global climate change have become a growing concern. Currently, most research is limited to the effects of a single factor such as light or moisture on plant growth and physiological processes (Huang et al. 2007; Zhang et al. 2002), while studies on interactions of soil moisture and light intensity on the growth, development and ecophysiological characteristics of *Amorpha fruticosa* seedlings have not been reported.

We selected the common deciduous shrub-*Amorpha fruticosa* to investigate the effects of soil moisture and light intensity on growth and ecophysiological characteristics. We sampled one-year old *Amorpha fruticosa* seedlings to provide theoretical guidance for water and light management in cultivation.

Materials and methods

Site and plant materials

Our experiment was conducted at Fanggan Research Station of Shandong University, Shandong Province, China (36°26'N,

117°27'E). The area has a warm temperate monsoon climate, with an average temperature of $13 \pm 1^\circ\text{C}$, and average annual precipitation of 700 ± 100 mm, most of which falls during summer. Dominant tree species are *Robinia pseudoacacia*, *Quercus acutissima*, *Pinus densiflora*, *Pinus tabulaeformis*, *Platycladus orientalis*, etc., and understory shrub layers are *Vitexnegundo* var. *heterophylla*, *Ziziphus jujube* var. *spinosa*, *Lespedeza davurica*, *Grewiabiloba* var. *parviflora*, etc. (Zhang et al. 2005). Mean photosynthetic photon flux density (PPFD) in the greenhouse was about 66% of the mean PPFD outside the greenhouse and the air in the greenhouse was well-ventilated by retracting the plastic side films. The vegetation type in this region is typical of warm temperate vegetation.

Mature and healthy seeds of *Amorpha fruticosa* were collected in November 2008 from the nearby hills at Fanggan and stored at $0\text{--}4^\circ\text{C}$ throughout the winter. The experiment lasted about five months from early April to late August 2009, which is the primary growth period of *Amorpha fruticosa* seedlings in a year. Seeds were soaked for 24 h before being germinated on moist pldget, and then the healthy and uniform seeds were selected and sown in 9-L plastic pots (32 cm \times 29 cm, height \times diameter) on 25 April. Sandy loam and humic soils were air-dried and mixed (5:2, v/v) as substrate for the pots. The mixture weighted about 8.0 kg dry weight per pot and the chemical properties were: organic matter $16.20\text{ g}\cdot\text{kg}^{-1}$, pH 6.16, total N $1.12\text{ g}\cdot\text{kg}^{-1}$, total P $1.72\text{ g}\cdot\text{kg}^{-1}$ and total K $21.81\text{ g}\cdot\text{kg}^{-1}$. The maximum saturated water content of the substrate was 34% by mass. All seedlings were well cultivated by conventional management before the start of the controlled experiments.

Experimental design

The control experiment began at the beginning of July. Four soil moisture levels were maintained at 80%–75% (W1), 60%–55% (W2), 40%–35% (W3), 20%–15% (W4) of the maximum saturated water content of substrates. The matrix water content was controlled through the whole basin weighing method. Two light treatment levels, full light in the greenhouse (L1) and shading (L2) were maintained by use of shade shelters covered by plastic films or woven black nylon nets. The average light intensities of the two light levels were 66% (no shade) and 10% (shaded) of the full light intensity in the field. Eight different treatment combinations were achieved with combinations of different soil moistures and light intensities. There were eight pots (repetitions) for each of the eight treatments. To minimize potential influences of environmental gradients within light treatments, the locations of pots within each light treatment were exchanged once a week. The control experiment lasted 50 days until late August.

Measurements and calculation

Morphological parameters such as height (H), basal diameter (BD, about 1 cm above the ground-line) and crown area ($\text{CA}=0.25\pi \times \text{crown length} \times \text{crown width}$) were measured and recorded every 10 days throughout the experiment. Plant biomass accumulation was determined by weighing at the end of the

experiment. Five pots of each treatment were tracked as repetitions.

Physiological indicators were measured. Photosynthetic parameters of each treatment were measured with CI-340 (CID, Inc, USA). Measurements were taken between 9:00 and 11:00 am on cloudless days. Three plants from each treatment of basically the same growth and apparent health were selected, and three blades per plant (without pests, showing similar growth, and representing similar illumination) were selected for sampling. Each blade was measured three times, and then net photosynthetic rate (Pn), transpiration rate (E), stomatal conductance (Gs), intercellular carbon dioxide concentration (InTCO₂) and other physiological parameters as well as photosynthetic active radiation (PAR) and atmospheric CO₂ concentration (CO₂ (in)) and other environmental parameters were automatically recorded by instruments. Water use efficiency was calculated according to the above parameters, $(\text{WUE}) = \text{Pn}/\text{E}$ (He et al. 2008). Stomatal limitation (Ls) was calculated based on the formula: $\text{Ls}=1-\text{InTCO}_2/\text{CO}_2(\text{in})$ (Berry and Downton 1982).

Photosynthetic pigment was extracted by ethanol extraction (Lichtenthaler and Wellburn 1983), the contents were determined and calculated with the method of Zhang et al. (2004).

Relative water content (RWC) was measured by weighing (Wang and Tao 1998), and then the water saturation deficit (WSD) was calculated. Leaf water loss rate was determined using the method of Zhang (1989). In each treatment, four pots were measured.

Statistical analysis

Data were tabulated using Excel 2003. Statistical analyses were performed using SPSS 13.0 software (SPSS Inc., IL, USA). Graphs were drawn by a professional graphics software Origin 7.5 (OriginLab Co., MA, USA).

Results

Morphological growth characteristics

During the treatment period, the height, basal diameter, and crown width of *A. fruticosa* seedlings showed gradually increasing trends (Fig. 1). Within light treatments, the amplitude of morphological indexes declined with the decreasing soil moisture.

Morphological parameters of the treated seedlings during the last period of the experiment are shown in Table 1. Within a given light treatment, morphological indices of height, basal diameter, crown width, total leaf area, and numbers of leaflets and compound leaves declined gradually with reduced soil moisture. Leaf-area index did not decline. Changes in morphological parameters varied significantly with soil moisture ($p<0.05$). When water supply was sufficient, the Plant Index of L1 light was greater than for L2 light. While with increasing water stress, seedling growth under light L2 began to exceed the level of L1, but most of morphological indices did not vary significantly.

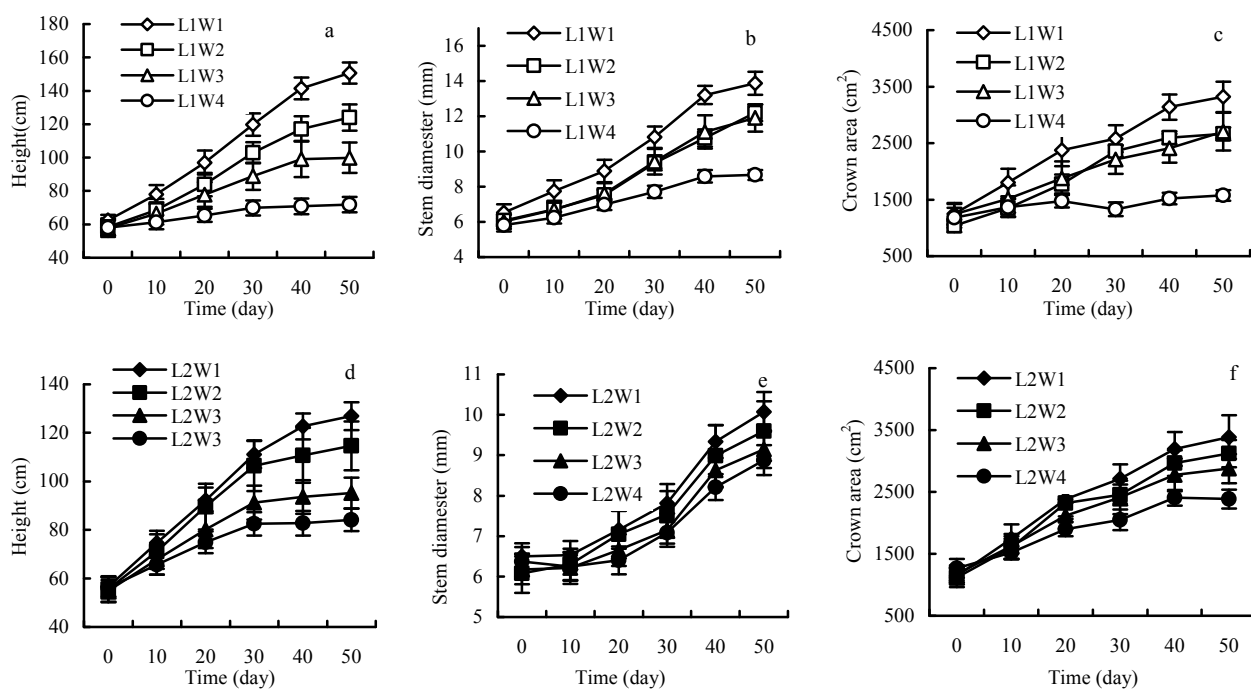


Fig. 1 Growth and morphological variables of *Amorpha fruticosa* seedlings during the experimental period. The error bars represent standard errors (SE) of the means. The data in the figure are means \pm SE ($n=8$). W1, soil moisture level at 80%–75%, W2 at 60%–55%, W3 at 40%–35%, W4 at 20%–15%; L1, full light in the greenhouse, L2, shading light in the greenhouse.

Table 1. Comparisons of morphological variables of *Amorpha fruticosa* L. seedlings under different water and light treatments at the end of the experimental period.

Treatment	Height (cm)	Stem diameter (mm)	Crown area (cm ²)	Total leaf area (cm ²)	Leaf area index	Leaf number	Compound leaf number
L1W1	150.59 \pm 6.34a*	13.87 \pm 0.65a*	3320.12 \pm 268.84a	4485.74 \pm 837.56a	1.51 \pm 0.42ns	1386.6 \pm 139.7a	68.8 \pm 4.3a
L1W2	124.04 \pm 7.81b	12.20 \pm 0.47b*	2663.06 \pm 114.77a	3707.76 \pm 458.67ab	1.36 \pm 0.17ns	1188.4 \pm 43.6ab	63.6 \pm 9.4ab
L1W3	95.90 \pm 9.12c	11.90 \pm 0.77b*	2702.74 \pm 333.54a	2644.31 \pm 335.29bc	0.83 \pm 0.12ns	894.0 \pm 129.9bc	49.6 \pm 5.3bc
L1W4	71.84 \pm 4.56d	8.66 \pm 0.28c	1573.79 \pm 95.61b*	1892.79 \pm 164.70c	1.22 \pm 0.14ns	637.2 \pm 54.7c	43.2 \pm 2.5c
L2W1	126.88 \pm 5.72a*	10.07 \pm 0.49ns*	3385.03 \pm 351.60a	3960.84 \pm 535.71a	1.13 \pm 0.21ns	1137.6 \pm 125.8a	66.2 \pm 11.8a
L2W2	114.64 \pm 10.08ab	9.60 \pm 0.74ns*	3119.25 \pm 217.97ab	3857.70 \pm 539.85a	1.10 \pm 0.13ns	1092.8 \pm 91.4ab	56.4 \pm 3.0ab
L2W3	95.18 \pm 6.34bc	9.15 \pm 0.46ns*	2875.90 \pm 237.40ab	2916.17 \pm 299.63ab	0.99 \pm 0.11ns	937.4 \pm 80.2ab	48.0 \pm 2.8ab
L2W4	84.13 \pm 4.61c	8.88 \pm 0.37ns	2383.69 \pm 152.67c*	2061.12 \pm 202.50b	0.84 \pm 0.12ns	795.8 \pm 78.2b	41.2 \pm 4.3b

The data are means \pm SE. $n=8$ for variables of the whole seedling and $n=20$ for variables of leaflet. Different letters in rows indicate significant differences ($p<0.05$) between different water treatments of the same light with Duncan multiple range test, ns means not significant. Asterisk indicate significant differences ($p<0.05$) between different light treatments. W1, soil moisture level at 80%–75%, W2 at 60%–55%, W3 at 40%–35%, W4 at 20%–15%; L1, full light in the greenhouse, L2, shading light in the greenhouse.

Photosynthetic and water use characteristics

Soil moisture and light intensity significantly affected the gas exchange parameters of *A. fruticosa* seedlings (Table 2). Under L1 light treatment, E decreased with declining soil moisture. $\ln\text{TCO}_2$ initially decreased and then increased, whereas L_s showed the opposite trend. E , $\ln\text{TCO}_2$, and L_s were significantly different between the four soil moisture treatments ($p<0.05$), while differences in P_n and G_s were not significant.

Under L2 light treatment, P_n , E , C declined with reduced soil moisture. $\ln\text{TCO}_2$ initially increased and then decreased, while L_s initially decreased and then increased, and all gas exchange parameters were significantly different between the four soil moisture treatments ($p < 0.05$). Within a given soil moisture treatment, most gas exchange parameters were significantly different between the two light treatments ($p < 0.05$), except P_n , G_s and $\ln\text{TCO}_2$ of W1 and G_s of W4.

Under L1 light treatment, Chla , $\text{Chla}+\text{b}$ declined with reduced soil moisture (Fig. 2). Chlb initially decreased and then increased,

but the opposite trend resulted for Chlb, Car and Car/Chl. Chlb, Chla+b, Chla/Chlb and Car/Chl varied significantly between the four soil moisture treatments ($p < 0.05$).

Table 2. The gas exchange parameters of *Amorpha fruticosa* L. seedlings under different treatments

Treatments	Net photosynthetic rate ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	Transpiration rate ($\text{mmol m}^{-2}\text{s}^{-1}$)	Stomatal conductance ($\text{mol m}^{-2}\text{s}^{-1}$)	Intercellular carbon dioxide concentration (μmolmol^{-1})	Stomatal limitation
L1W1	9.44±2.83ns	2.62±0.45a*	296.85±81.25ns	467.06±6.91a	0.10±0.02b*
L1W2	8.09±1.22ns*	2.14±0.31ab*	181.08±37.85ns*	434.98±4.51b*	0.16±0.01a*
L1W3	8.46±1.31ns*	2.00±0.20ab*	191.33±31.02ns*	436.37±3.42b*	0.15±0.01a*
L1W4	5.64±0.64ns*	1.58±0.13b*	178.62±21.13ns	458.43±2.38a*	0.11±0.01b*
L2W1	2.75±0.12a	1.02±0.10a*	327.11±82.88a	469.92±2.18c	0.04±0.01a*
L2W2	2.69±0.06a*	1.11±0.04a*	352.94±25.50a*	476.97±0.77a*	0.03±0.00b*
L2W3	2.42±0.19a*	1.12±0.05a*	356.20±24.68a*	475.34±0.80ab*	0.03±0.00b*
L2W4	1.22±0.07b*	0.76±0.03b*	132.84±5.23b	472.30±0.88bc*	0.03±0.00ab*

The data in the table are means \pm SE (n=9). Different letters in rows indicate significant differences ($p < 0.05$) between different water treatments of the same light with Duncan multiple range test, ns means not significant. Asterisk indicate significant differences ($p < 0.05$) between different light treatments. W1, soil moisture level at 80%–75%, W2 at 60%–55%, W3 at 40%–35%, W4 at 20%–15%; L1, full light in the greenhouse, L2, shading light in the greenhouse.

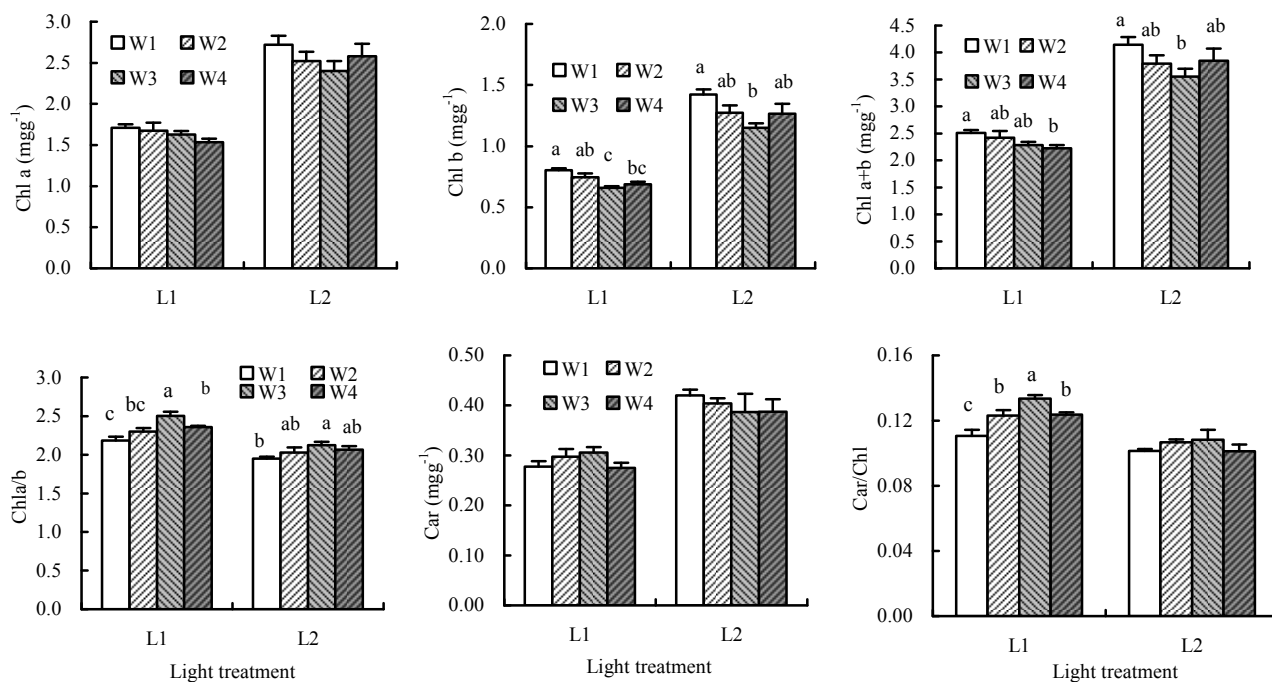


Fig. 2 The effect of treatments on the photosynthetic pigment content of *Amorpha fruticosa* seedlings. The data are means \pm SE (n=4). W1, soil moisture level at 80%–75%, W2 at 60%–55%, W3 at 40%–35%, W4 at 20%–15%; L1, full light in the greenhouse, L2, shading light in the greenhouse.

Under L2 light treatment, Chla, Chlb, Chla+b and Car initially decreased and then increased, while Chla, Chlb and Car/Chl showed the opposite trend. Only Chlb, Chla+b and Chla/Chlb varied significantly with soil moisture treatment ($p < 0.05$). Chla, Chlb, Chla+b and Car under higher light intensity were lower than under lower light intensity, while Chla/Chlb and Car/Chl were higher. The difference between the two light intensities was significant ($p < 0.05$), which showed low light favored the increase of photosynthetic pigment.

Water use characteristics of the treated leaves are shown in Fig. 3. Leaf water saturation deficit gradually and significantly in-

creased with the reduction of soil moisture ($p < 0.05$). At a given soil moisture, leaf water saturation deficit in L1 light treatment was greater than in L2, but the change under different light intensities was not significant. Under L1 light treatment, WUE initially increased and then decreased with declining soil moisture. WUE was greatest at W3 soil moisture. Under L2 light treatment, WUE decreased significantly with declining soil moisture ($p < 0.05$). WUE decreased with declining light intensity ($p < 0.05$) between soil moisture treatments of W2, W3 and W4. Leaf water loss increased sharply with increasing stress time. Water loss rates were above 70% for all leaves stressed for six

hours. Within a given light treatment, the leaf water loss rate of

W4 was less than for the other three treatments.

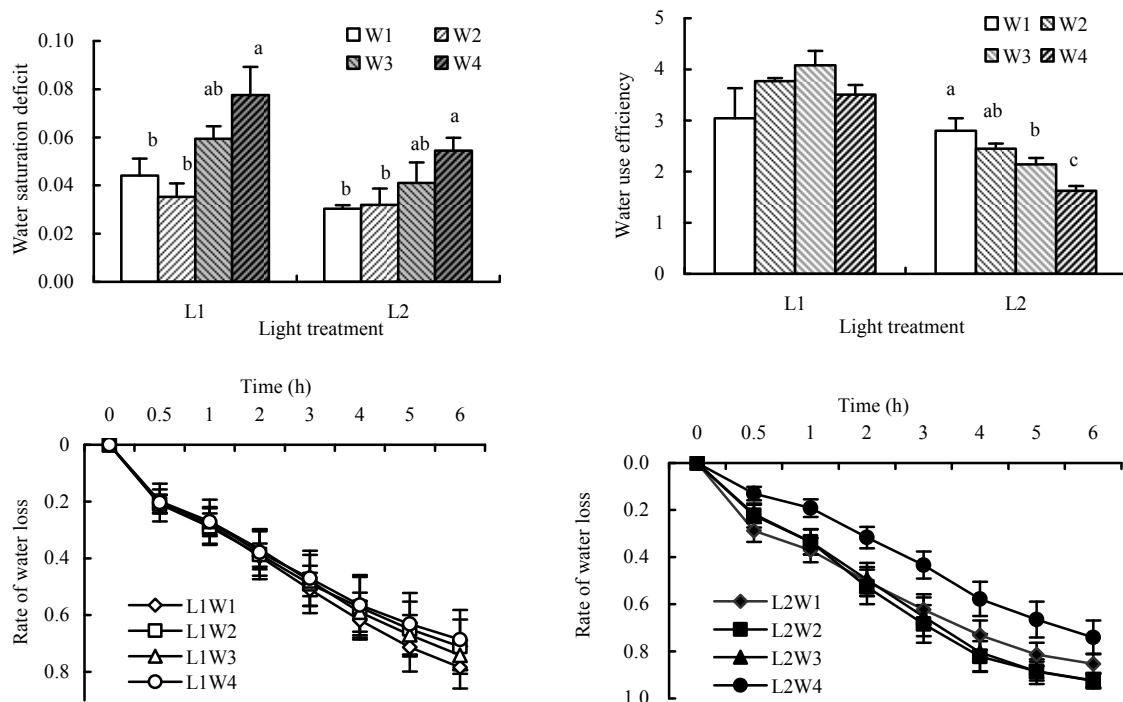


Fig. 3 Water use characteristics of *Amorpha fruticosa* L. seedlings under differing water and light treatments. The data are means \pm SE. $n=(3-4)$. W1, soil moisture level at 80%–75%, W2 at 60%–55%, W3 at 40%–35%, W4 at 20%–15%; L1, full light in the greenhouse, L2, shading light in the greenhouse.

Biomass accumulation and allocation

Reduced soil moisture decreased total biomass, stem biomass, leaflet biomass and compound petiole biomass accumulation (Fig. 4), and was closely correlated with stress intensity ($p < 0.05$). Biomass accumulation of plant parts was positively correlated with light intensity, but weakly correlated with soil moisture. There was a negative correlation between root mass ratio and soil moisture, and a positive correlation between stem mass ratio and moisture stress ($p < 0.05$). Leaf mass ratio and the ratio of taproot to lateral root did not change significantly with soil moisture, but there was a significant increase in shoot ratio ($p < 0.05$). At a given soil moisture content, the root mass ratio and shoot ratio under L1 light intensity were greater than under L2 ($p < 0.05$). Other allocation indicators of L2 light treatment were greater than L1.

Discussion

Morphological adaptation

Light and water are necessary resources for plant growth. Water stress and light significantly impacted growth of *A. fruticosa* seedlings. Water stress significantly limited the vertical and radial growth of *A. fruticosa* seedlings. When water supply was

sufficient, the seedlings grew well and produced more leaflets and greater total leaf area, which means larger cover and abundant sunlight for growth (Jin et al. 2005). Strong light is conducive to more active photosynthesis of *A. fruticosa* seedlings, thus seedlings achieve greater height, larger crown size and more numerous leaves with larger leaf area. When the water supply is insufficient, plants can use the limited water to survive but growth is inhibited. Shade would reduce water evaporation, so plants can use the limited water for survival and slow growth. Plants adopt different resource use strategies under different environmental circumstances, which not only ensures the survival of plants, but also maintains maximum growth.

Photosynthetic adaptation

Leaf photosynthesis is the basic unit of accumulation and physiological metabolism in the process of plant production (Zheng and Yang 2006). The effects of water and light on plant growth are largely attributed to their effects on plant photosynthesis and transpiration. This study showed that, at a given light intensity, the net photosynthetic rate of *A. fruticosa* seedlings declined with increasing water stress. Excessive light absorption caused by inadequate water supply and increased leaf temperature caused by reduced transpiration both cause a certain degree of damage to the photosynthetic apparatus, which would reduce the stomatal regulation of gas exchange. In order to adapt to water shortage and maintain internal water balance, *A. fruticosa* seedlings could

only reduce the photosynthetic capacity of mesophyll cells (Guo et al. 2003). At a given soil moisture content, net photosynthetic rate and transpiration rate of *A. fruticosa* seedlings in strong light were significantly higher than that in the shaded treatments. A

reason might be that in strong light, the seedlings provide sufficient raw materials for photosynthesis by maintaining more vigorous transpiration.

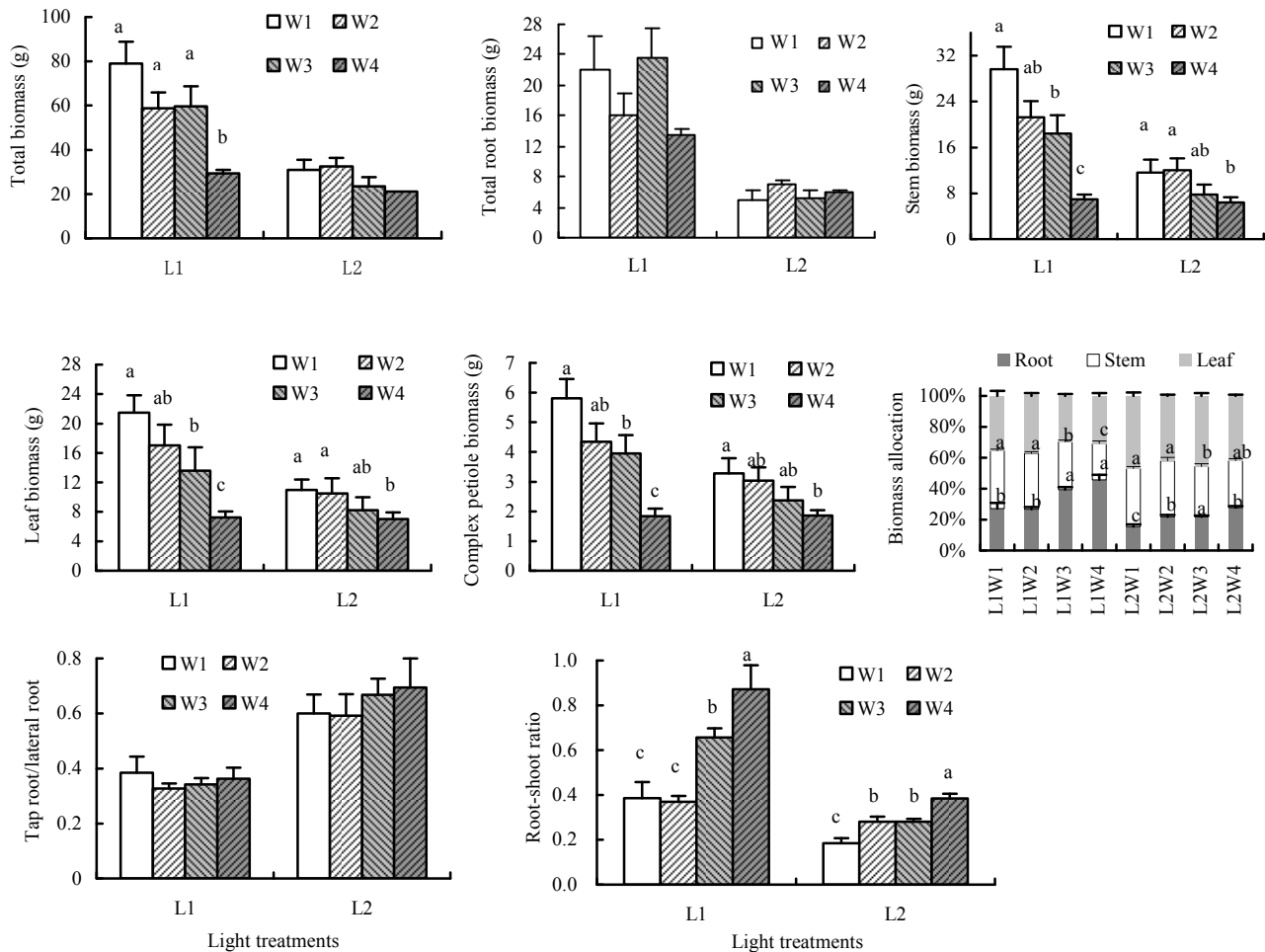


Fig. 4 Comparisons of biomass accumulation and allocation of *Amorpha fruticosa* seedlings under differing water and light treatments. The data are means \pm SE (n=5). W1, soil moisture level at 80%–75%, W2 at 60%–55%, W3 at 40%–35%, W4 at 20%–15%; L1, full light in the greenhouse, L2, shading light in the greenhouse.

Change of photosynthetic pigment content

Plant chlorophyll content is an important indicator of plant growth status. Chlorophyll content is strongly correlation with plant photosynthetic capacity (Tjus et al. 1999). Water treatments affected the chlorophyll content of *A. fruticosa* leaves: when water supply was sufficient, chlorophyll content was high and chlorophyll a/b value was low, which was conducive to capture and full use of light. As water stress increased, chlorophyll content of the leaves declined and chlorophyll a/b value increased slightly. This was probably due to leaf water loss affecting the synthesis of chlorophyll and promoting accelerated decomposition of formed chlorophyll. At a given soil moisture content, chlorophyll a, chlorophyll b and total chlorophyll content of

shaded *A. fruticosa* seedlings were significantly higher than under strong light treatment. Chlorophyll a/b was lower than under strong light treatment, which improved seedling ability to absorb and transfer light energy, and fully use light energy under low light conditions, indicating *A. fruticosa* has a degree of shade tolerance.

Carotenoid, which has a common synthetic precursor with chlorophyll, plays an important role in the photosynthesis in chloroplasts (Krause 1988). Carotenoid also protects the photosynthetic apparatus of carotenoids (Ma and Cheng 1997), thereby protecting plants against various types of stress damage (Ji et al. 2007; Willekens et al. 1994). In this study, there was no significant difference in carotenoid content of stressed leaves between soil moisture treatments, but there were significant differences between light treatments. The carotenoid content of shaded *A.*

fruticosa seedlings was higher than for seedlings under strong light treatment. This might be due to blockage of photosynthesis under shade, which leads to the accumulation of excess excitation energy. By accelerating the synthesis of carotenoids and dissipating excess excitation energy of heat which cannot be consumed by photosynthesis, plants can, to some extent, alleviate the damage to the photosynthetic system caused by low-light stress. This result is consistent with previous studies (Yamamoto 1975).

Water conversation and use

Water use efficiency reflects the relationship between plant water consumption and its dry matter production, which is an integrated physiological and ecological indicator reflecting the suitability of plant growth (Zhang and Shan 2002). Some evidence shows that when plants are in mild and moderate drought stress, WUE increases gradually with increasing water stress, while as drought stress further increases, WUE declines (Li et al. 2002; Zhao et al. 2003). This is consistent with the results of strong light treatments in this study. In shade treatments, WUE decreased significantly with increasing water stress. Higher soil moisture and lower light intensity lead to higher leaf relative water content and smaller water saturation deficit, which reduce influences on normal physiological activities of plants.

The leaf blade dehydration rate is used to express the anti-dehydration ability of plant tissues. Serious water stress in combination with shade led to reduced leaf water loss rates, indicating that drought and shade induced higher capacity of water conversation.

Biomass accumulation and allocation adaptation

Biomass is the main manifestation of the ability of plants to gain energy and has an important influence on plant development and structure formation (Xiao et al. 2004). In growth and development, plants continually adjust growth and biomass allocation strategies to adapt to environmental change. Our findings indicated that, under strong light intensity, total biomass accumulation and plant part biomass accumulation of *A. fruticosa* seedlings gradually declined with declining soil moisture. In shade treatments, the biomass accumulation in W2 treatment was greatest, indicating that in shade treatments, the soil moisture level maintaining optimal growth dropped, and excessively high or low water content was not conducive to growth and dry matter accumulation. Biomass accumulation of plants under low light intensity was lower than that under high light intensity, and this difference was not significant at higher levels of water stress. This reflects the tradeoff between acquisition and utilization of water and light, a result of the interaction between soil moisture and light intensity.

Plant parts have various ecological functions. Biomass allocation of each part depends upon growth regulation and material allocation strategies (Yang and Li 2003). When water supply was sufficient or plants were shaded, *A. fruticosa* seedlings allocated more biomass to stems and leaves for aerial growth. This im-

proved photosynthetic capacity and met the needs for consumption and growth of plants. While in water stress and strong light, plants formed well-developed root systems through allocating more biomass to root growth. This not only improved acquisition and utilization rates of soil moisture, but also reduced water loss caused by transpiration, helping plants survive in drought conditions (Guo et al. 2007).

In summary, *A. fruticosa* seedlings regularly adjust their morphological growth and physiological activities to achieve full utilization of water and light resources. This indicates that the species has a strong potential ability to adapt to water and light stress, which is important for *A. fruticosa* seedling survival and growth in dry environments and heterogeneous light conditions.

References

- Berry JA, Downton WJS. 1982. Environmental regulation of photosynthesis. In: Govindjee (ed.), *Photosynthesis*. New York: Academic Press, 263–343.
- Bertamini M, Neduncheanian N. 2003. Photoinhibition of photosynthesis in mature and young leaves of grapevine. *Plant Science*, **164**(4): 635–644.
- Guo WH, Li B, Zhang XS, Wang RQ. 2007. Architectural plasticity and growth responses of *Hippophae rhamnoides* and *Caragana intermedia* seedlings to simulated water stress. *Journal of Arid Environments*, **69**: 385–399.
- Guo XY, Yang YF, Li JD. 2003. Research on photosynthetic characteristics of reed in different dry habitats of Songnen plain. *Acta Prataculturae Sinica*, **12**(3): 16–21.
- He CX, Li JY, Guo M, Wang YT, Chen C. 2008. Changes of leaf photosynthetic characteristics and water use efficiency along tree height of four tree species. *Acta Ecologica Sinica*, **28**(7): 3008–3016.
- Huang J, Guo SR, Wu Z, Huang J, Guo SR, Wu Z, Li SJ. 2007. Effects of weak light on photosynthetic characteristics and chloroplast ultrastructure of non-heading Chinese cabbage. *Chinese Journal of Applied Ecology*, **18**(2): 352–358 (in Chinese).
- Ji WD, Shi GX, Yang HY, Xu QS, Xu Y, Zhang H. 2007. Effects of Cu²⁺ stress on leaf physiological indice and ultrastructure of *Potamogeton malaianus*. *Chinese Journal of Applied Ecology*, **18**(12): 2727–2732.
- Jin J, Zhong ZC, Liu JC, He YJ. 2005. Response of the phenotypic plasticity of *Cajanus cajan* seedlings to relative soil water content in limestone areas. *Journal of Southwest Agricultural University (Natural Science)*, **27**(1): 89–92.
- Krause GH. 1988. Photoinhibition of photosynthesis—An evaluation of damaging and protective mechanisms. *Physiologia Plantarum*, **74**: 566–574.
- Lichtenthaler HK, Wellburn AR. 1983. Determination of total carotenoids and chlorophylls a and b of leaf extracts in different solvents. *Biochemical Society Transactions*, **11**: 591–592.
- Li JY, Zhou P, Zhao LJ. 2002. Influence of drought stress on transpiring water-consumption of seedlings. *Acta Ecologica Sinica*, **22**(9): 1380–1386.
- Ma JY, Zhou R, Cheng BS. 1997. The relationship between Carotenoids and reactive nitrogen metabolism. *Journal of Shandong Agricultural University*, **28**(4): 518–522.
- Pell EJ, Sinn JP, Eckardt N, Johansen CV, Winner WE, Mooney HA. 1993. Response of radish to multiple stresses. II. Influence of season and genotype on plant response to ozone and soil moisture deficit. *New Phytologist*, **123**(1): 153–163.

- Tjus SE, Moiler BL, Scheller HV. 1999. Photoinhibition of photosystem I damage both reaction center proteins PS I-A and PS I-B and acceptor side located small photosystem I polypeptides. *Photosynthesis Research*, **60**: 75–86.
- Wang M, Tao DL. 1998. Drought-tolerance of main tree species in Changbai Mountain. *Chinese Journal of Applied Ecology*, **9**(1): 7–10.
- Willekens H, Camp WV, Montagu MV, Inze D, Langebartels C, Jr HS. 1994. Ozone, sulfur dioxide and ultraviolet- B have similar effects on mRNA accumulation of antioxidant genes in *Nicotiana plumbaginifolia* L. *Plant Physiol*, **106**: 1007–1014.
- Xiao DM, Wang M, Ji LZ. 2004. Influence of water stress on growth and biomass allocation of dominant tree species in mixed forest of broad-leaved and Korean pine at Changbai Mountain. *Chinese Journal of Ecology*, **23**(5): 93–97.
- Yamamoto HY. 1975. Biochemistry of the violaxanthin cycle in higher plants. *Pure and Applied Chemistry*, **51**: 639–648.
- Yang YF, Li JD. 2003. Biomass allocation and growth analysis on the ramets of *Phragmites amumis* populations in different habitats in the Songnen Plains of China. *Chinese Journal of Applied Ecology*, **14**(1): 30–34.
- Zhang SQ, Shan L. 2002. Plant water use efficiency and its research progress. *Agricultural Research in the Arid Areas*, **20**(4): 1–5.
- Zhang SR, Gao RF, Wang LJ. 2004. Response of oxygen evolution activity of photosystem II, photosynthetic pigments and chloroplast ultrastructure of hybrid poplar clones to light stress. *Acta Phytoecologica Sinica*, **28**(2): 143–149.
- Zhang XF, Yu XC, Zhang ZX. 2002. Effect of soil water on the growth and physiological characteristics of grafted and non-grafted cucumber in greenhouse. *Chinese Journal of Applied Ecology*, **13**(11): 1399–1402 (in Chinese)
- Zhang XZ. 1989. Experimental techniques in plant physiology. Shenyang: Liaoning Science and Technology Press, 47–48.
- Zhang YL, Zhang XQ, Wang RQ. 2005. Preliminary studies on the flora in the Luzhong Mountains. *Journal of Shandong Forestry Science and Technology*, **34**(1): 1–5.
- Zhang ZA, Zhang MS, Wei RH. 2004. Experimental guide of plant Physiology. Beijing: Chinese Agricultural Science and Technology Press, 64–68.
- Zhao LJ, Li JY, Yu JF, Bertin S. 2003. Daily variation in transpiring water-consumption rates of seedlings in different drought stress. *Journal of Beijing Forestry University*, **25**(3): 42–47.
- Zheng SH, Yang CR. 2006. The ecophysiological and morphological characteristics of maize in seedling stage under water stress. *Acta Ecologica Sinica*, **26**(4): 1138–1143.